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The Freshwater Gastropods of Iowa (1821-1998): Species Composition, Geographic Distributions, and Conservation Concerns

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Keywords
biogeography, Gastropoda, endangered species, macroinvertebrates, snails

Comments
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The freshwater gastropods of Iowa (1821-1998): Species composition, geographic distributions, and conservation concerns

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Abstract: Although gastropods are important members of freshwater communities, the geographic range, ecological requirements, and conservation status of most species are poorly known. To advance this understanding, I used survey data from museums and peer-reviewed literature to summarize knowledge of the taxonomic composition and geographic distributions of freshwater gastropods in Iowa, U.S.A. Excluding records likely based on erroneous reports, 49 freshwater gastropod taxa (47 species and 2 genera with unknown numbers of species) inhabited Iowa during all or part of the period when records were collected (1821-1998). The Mississippi River and nearby tributaries of eastern Iowa and the prairie pothole and kettlehole regions of northern Iowa historically supported a large number of taxa. In contrast, few gastropods have been reported from the loess soils ecoregion of southwestern Iowa. Although recent improvements in water quality and increases in wetland habitat have likely benefited many gastropod taxa, it appears that as many as 18 species are now imperiled or extirpated from Iowa, and an additional 7 species were much less widespread at the end of the 20th century than formerly. These 25 species of conservation concern were identified on the basis of rarity or absence of recent records and on evidence of local extinctions that were associated with pollution and habitat loss. By comparing data summarized in this review with future data from field surveys, evidence of restricted or shrinking geographic ranges can be provided, and the true conservation status of Iowan gastropods will be determined. This information is of critical importance in establishing legal protection and action plans for the recovery of endangered species.

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Gastropods constitute a high percentage of the macroinvertebrate biomass in many freshwater benthic habitats, and their dramatic effects on ecosystem and community dynamics are well documented (Brönmark and Vermaat 1998, Brown 2001). These snails occupy a central position in food webs; they graze on periphyton and detritus, and in turn are consumed by a variety of invertebrate and vertebrate predators (Dillon 2000, Brown 2001). When gastropods are abundant, they regulate benthic primary productivity and algal community structure, and function as important conduits of energy- and nutrient-flow from microorganisms and decomposing organic matter to fish and wildlife (Brönmark and Vermaat 1998, Brown 2001).

Despite ample evidence that freshwater gastropods are ecologically important, we have a poor understanding of the geographic distribution, environmental requirements, and conservation status of most North American species (Neves *et al.* 1997, Bogan 1998). Relative lack of attention to the natural history and taxonomy of freshwater gastropods are key reasons for our weak knowledge base. More than 180 years after Thomas Say published the first descriptions of North American freshwater gastropods, taxonomic confusion still makes it impossible to quantify accurately the geographic ranges and population sizes for many species (Say 1817, Neves *et al.* 1997, Dillon *et al.* 2002). Additionally, federal and state natural resource agencies generally have little interest in freshwater gastropods, and lack of studies of gastropod ecology and geographic distribution is attributed, in large part, to lack of financial support (Neves *et al.* 1997).

Clearly, neglect of freshwater gastropods has proved costly. At least 42 species have become extinct following European settlement of North America (Neves *et al.* 1997, Bogan 1998). Twenty of the remaining 500-600 species are considered by the United States government to be threatened or endangered, and approximately 200 species were recently listed as candidates for inclusion on the federal list of endangered and threatened species (Neves *et al.* 1997, Bogan 1998, U.S. Fish and Wildlife Service 2005). These and other species of freshwater gastropods are thought to have experienced dramatic population declines, but quantitative evidence needed to facilitate legal action and recovery plans are rarely available (Angelo *et al.* 2002, Stewart and Dillon 2004).

Field surveys provide critical evidence of changes in freshwater gastropod assemblages, including population declines and shrinking or restricted geographic ranges. Although large quantities of survey data exist for many North American species, these data are usually scattered among museum collections and literature that can be difficult to obtain. These data must be summarized and disseminated to obtain an accurate assessment of the geographic distribution and conservation status of freshwater gastropods.

I reviewed and summarized data from field surveys in museum databases and peer-reviewed literature to describe

the species composition and geographic distribution of freshwater gastropods in Iowa, U.S.A. Geographic information associated with collection records was used to produce maps and narrative descriptions of distributions of species inhabiting Iowa now or historically. Additionally, I identified species of potential conservation concern on the basis of rarity or absence of recent records and historical evidence of local extinctions. This is the first comprehensive review of knowledge regarding Iowa's freshwater gastropods, and is part of a recent initiative to determine the species composition and conservation status of freshwater gastropods in all North American states and provinces (Freshwater Mollusk Conservation Society 2005).

METHODS

Study area

Iowa is situated in the middle interior of the United States and is considered one of the northern Great Plain states. Iowa extends from 40°35′N to 43°30′N in latitude, from 89°5′W to 96°31′W in longitude, and encloses a total area of 145,003 km^2 (Prior 1991, Tobin 2000). Most of the landscape is characterized by low relief and rolling hills, but the Paleozoic Plateau of northeastern Iowa is a notable exception, consisting of rugged terrain with abundant limestone cliffs (Prior 1991). Elevation in the state ranges from 145-509 m above sea level (Tobin 2000).

Iowa's climate is characterized by hot summers and cold winters. Annual temperatures average 8-11°C, but extremes of −44°C and 48°C have been recorded (Tobin 2000). The state receives an annual average of 81 cm of precipitation. Moderate precipitation, in combination with fertile soils derived from glacial drift and subsequent weathering processes, enabled Iowa to become one of the most productive agricultural regions in the world (Prior 1991, Tobin 2000). Almost 95% of the land surface is now used for farming (Tobin 2000). Farms replaced almost all of the tallgrass-prairie grasslands and forests that dominated the terrestrial landscape at the time of European settlement.

Agriculture and other anthropogenic activities have also impacted Iowa's freshwater ecosystems. Up to 99% of the original 31,000 km^2 of wetlands constituting the prairie pothole complex in northern Iowa were lost to agriculture and development (Bishop *et al.* 1998, Euliss and Mushet 1999). However, wetland habitat is again increasing in Iowa, with at least 240 km^2 of prairie pothole wetlands restored since 1988 (Bishop *et al.* 1998). Similarly, pollution from sewage and industrial effluent has degraded many lakes and rivers, but recent improvements in technology for the treatment of wastewater have had positive effects on water quality in these ecosystems (Shimek 1935a, Bovbjerg *et al.* 1982). Water quality in Iowa's large lakes is of particular concern. These ecosystems are few in number and lakes occurring in the kettlehole region of northcentral and northwestern Iowa provide the only known habitat in Iowa for many species (Shimek 1915, Shimek 1935a). In contrast to large lakes, rivers are abundant. The Mississippi and Missouri River drainages represent Iowa's two major watersheds (Fig. 1A). Rivers in eastern Iowa flow toward the southeast and empty into the Mississippi River, which constitutes the eastern boundary of the state. Western rivers flow toward the southeast to the Missouri River, which represents Iowa's western border (Prior 1991, Tobin 2000).

Study design

Gastropod distributional information was obtained from peer-reviewed literature and museum records that were available as of January 2004. I reviewed any refereed publication that might contain distributional data for freshwater gastropods in Iowa. A total of 910 publications were

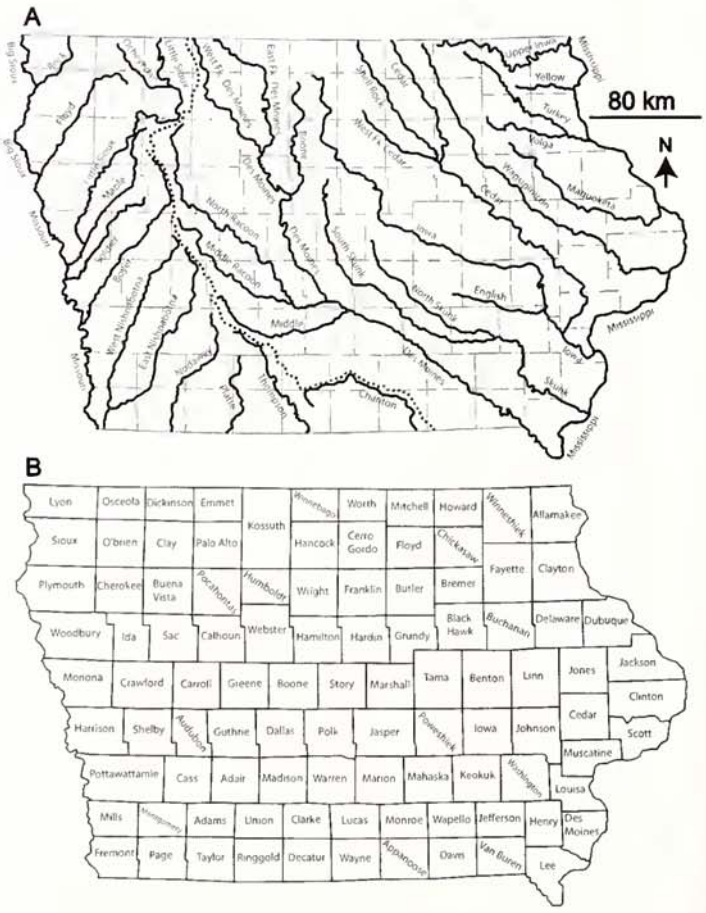

Figure 1. The (A) major rivers and (B) counties of Iowa. The dark dashed line in (A) represents the boundary of the Mississippi River-Missouri River watersheds (maps adapted from Prior 1991 and constructed using Adobe Illustrator® 10 for Windows®)

reviewed; 74 of these contained records of freshwater gastropods from Iowa. Museum records were obtained from curatorial staff or databases available on the World Wide Web. I requested records from 40 North American museums known to have molluscan collections; 13 museums provided electronic records of freshwater gastropods collected in Iowa (Table 1).

A map and/or narrative description of geographic distribution was produced for each taxon recorded from Iowa since living freshwater gastropods were first reported in the 19th century. Counties and specific localities of occurrence were the geographical units used to construct maps (Fig. 1B). Distribution maps using watersheds as basic units might reveal more ecological information than maps using counties. However, specific watershed information was rarely included with historical records, whereas counties and other political units were often reported.

Habitat-use descriptions of taxa are included if this information was provided with records. Evidence of temporal change in distribution and abundance of a taxon is also discussed, along with hypothesized causes provided by investigators observing these changes. Maps were not constructed for species I consider to be erroneously reported from Iowa, but rationale for my decisions are provided. Unless otherwise indicated, taxon names and their authorities are based on Turgeon *et al.* (1998).

RESULTS

Results suggest that 49 freshwater gastropod taxa inhabit Iowa now or occurred there at some time during the period when accessible records were collected (1821-1998). These taxa include 47 species and 2 genera with unknown numbers of species. Additionally, I uncovered records of 6 species that I conclude were reported in error (Table 2).

Family Valvatidae

Valvata bicarinata (Lea, 1841). Individuals of *V. bicarinata* were reported from lentic habitats in southeastern and northwestern Iowa (Fig. 2A; Keyes 1888, Shimek 1890, Walker 1902, 1918, Shimek 1915, Baker 1928, BMNH, FMNH). Population changes for this and several other species have been documented by surveys of Lake Okoboji and nearby habitats of Dickinson County in northwestern Iowa. Shimek (1915) reported *V. bicarinata* from deeper waters of Lake Okoboji, the Gar lakes, and nearby ponds and wetlands. However, it was not found in subsequent surveys of Lake Okoboji that were conducted in 1933-1934, 1954-1959, and 1979 (Shimek 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982). The probable loss of *V. bicarinata* from Lake Okoboji is consistent with the nearly complete destruction of gastropods in that lake between 1915 and 1933 (Shimek 1915, Shimek 1935a). Shimek (1935a) attributed striking declines in the abundance and diversity of gastropods to the degradation of water quality caused by discharge of sewage into the lake.

Valvata lewisi (Currier, 1868). Shimek (1915) reported that *V. lewisi* formerly occurred in the Okoboji region of Dickinson County in northwestern Iowa, but considered this species to be extinct in that region by 1915. I found no other records of *V. lewisi*.

Table 1. Museums with records of freshwater gastropods from Iowa. Abbreviations are used in the text to indicate sources of records. Data sources were accurate as of February 2005.

Museum	Abbreviation	Data source
J. Ford Bell Museum of Natural History	BMNH	Jonathan Slaght (Freshwater Mollusk Collection Manager)
California Academy of Sciences, San Francisco	CAS	Robert Van Syoc (Senior Collection Manager, Invertebrates)
Cincinnati Museum Center	CMC	Steve Matter (Curator of Zoology)
Cleveland Museum of Natural History	CMNH	Joseph Keiper (Curator of Invertebrate Zoology)
Carnegie Museum of Pittsburgh	CMP	Tim Pearce (Assistant Curator and Head of Mollusk Section)
Delaware Museum of Natural History	DMNH	Kevin Roe (Curator of Mollusks)
Florida Museum of Natural History	FMNH	http://www.flmnh.ufl.edu/natsci/malacology/malacology.htm
Illinois Natural History Survey	INHS	http://www.inhs.uiuc.edu/cbd/collections/mollusk/molluskintro.html
Milwaukee Public Museum	MPM	Joan Jass (Curator of Non-insect Invertebrates)
North Carolina State Museum of Natural Sciences	NCM	Arthur Bogan (Curator of Aquatic Invertebrates)
National Museum of Natural History, Smithsonian	NMNH	Linda Ward (Department of Systematic Biology, Invertebrate Zoology)
Ohio State Museum of Biological Diversity	OSM	Thomas Watters (Curator of Molluscs)
Santa Barbara Museum of Natural History	SBM	Paul Scott (Curator of Malacology)

Table 2. Species reported from Iowa, whose occurrence there between 1821 and 1998 is doubtful.

Species	Records (and references)	Rationale for conclusion
Fontigens nickliniana (Lea, 1838)	Mississippi River, Lee County (Jude 1973, Thompson 1973, Gale 1975)	In a review of *Fontigens*, Hershler *et al.* (1990) reported no legitimate records from Iowa or the upper Mississippi River
Somatogyrus amnicoloides (Walker, 1915)	Eldora in Hardin County and the Cedar River at Cedar Falls, Black Hawk County (FMNH)	Known only from the Ouachita River, Arkansas (Burch 1989)
Elimia semicarinata (Say, 1829)	Mississippi River at Muscatine, Muscatine County (FMNH)	An eastern species occurring as far west as Ohio and Kentucky (Burch 1989)
Pleurocera canaliculata (Say, 1821)	Iowa (CMC)	Although a record occurs from Nebraska, this species appears to be restricted to the Ohio and Wabash watersheds (Burch 1989)
Gyraulus albus (Müller, 1774 in Baker 1928)	Davenport in Scott County, Des Moines in Polk County, Cedar Lake at Cedar Rapids in Linn County, and the Lake Okoboji region of Dickinson County (Keyes 1888, Shimek 1893, 1915)	A European species morphologically similar to *Gyraulus deflectus* (Baker 1928, 1945)
Ancylus fluviatilis (Müller, 1774 in Baker 1928)	Davenport, Scott County (Pratt 1876)	A European species (Baker 1928)

Valvata sincera (Say, 1824). Tryon (1870-1871) reported *V. sincera* from an unspecified location in Iowa. I found no other records for this species.

Valvata tricarinata (Say, 1817). Individuals of *V. tricarinata* have been collected from swamps, ponds, lakes, and rivers across Iowa (Fig. 2B; Say 1821, Haldeman 1840-1845, Binney 1865a, Tryon 1865, Pratt 1876, Witter 1878, Shimek 1890, 1915, 1935a, Bardach *et al.* 1951, Bovbjerg and Ulmer 1960, Gale *et al.* 1972, Thompson 1973, Gale 1975, Bovbjerg *et al.* 1982, Coleman 1984, BMNH, FMNH). Historical population trends of *V. tricarinata* in Lake Okoboji mirror the decline and subsequent recovery of water quality in Okoboji and other large northwestern Iowa lakes following improvements in sewage treatment (Bovbjerg *et al.* 1982). Shimek (1915) originally reported *V. tricarinata* to be abundant in both shallow and deep waters of Lake Okoboji, but by 1933-1934 this species was not found in that lake (Shimek 1935a). By the 1950s, *V. tricarinata* was again increasing in abundance in Lake Okoboji, but did not occur at depths exceeding 10 m (Bovbjerg and Ulmer 1960). By 1979, *V. tricarinata* was abundant and had recolonized depths exceeding 20 m (Gale *et al.* 1972, Bovbjerg *et al.* 1982).

Family Viviparidae

Viviparus georgianus (=*Vivipara contectoides*, *Viviparus contectoides*) (Lea, 1834). Individuals of *V. georgianus* are known only from Lee County in extreme southeastern Iowa. This species was recently reported from a lagoon near Montrose and multiple locations in the Mississippi River from Keokuk to 5 km north of Fort Madison (Fig. 2C; Thompson 1973, Gale 1975, FMNH).

Viviparus intertextus (=*Vivipara intertexta*) (Say, 1829). *Viviparus intertextus* is also restricted to the Mississippi River watershed. It has been recorded from slow-flowing areas of the Cedar and Mississippi Rivers and from bayous and sloughs in Lee and Muscatine counties (Fig. 2D; Tryon 1863, 1865, 1870-1871, Binney 1865a, Pratt 1876, Witter 1878, Baker 1905, 1928, Clench and Fuller 1965, Carlson 1968, FMNH, OSM).

Viviparus subpurpureus (=*Vivipara subpurpurea*) (Say, 1829). This viviparid has been reported from several locations within the Mississippi River, where it occurs in rather swift water and inhabits hard substrates (Fig. 2E; Pratt 1876, Shimek 1890, Call 1894, Baker 1905, 1928, Clench and Fuller 1965, FMNH, INHS).

Bellamya chinensis (=*Viviparus chinensis*, *Viviparus malleatus*) (Reeve, 1863). Formerly known as *Cipangopaludina chinensis*, this Asian snail was first reported from Iowa in the mid-1970s from Riverview Park Lagoon, near the Des Moines River in Des Moines, Polk County (Barnhart 1978, Smith 2000). Jokinen (1982) also reported it from an unspecified location in Des Moines.

Campeloma spp. (=*Campeloma coarctatum*, *Campeloma crassulum*, *Campeloma decisa*, *Campeloma decisum*, *Campeloma exilis*, *Campeloma integra*, *Campeloma integrum*, *Campeloma milesi*, *Campeloma milesii*, *Campeloma obesum*, *Campeloma ponderosum*, *Campeloma regulare*, *Campeloma rufum*, *Campeloma subsolida*, *Campeloma subsolidum*, *Cam-*

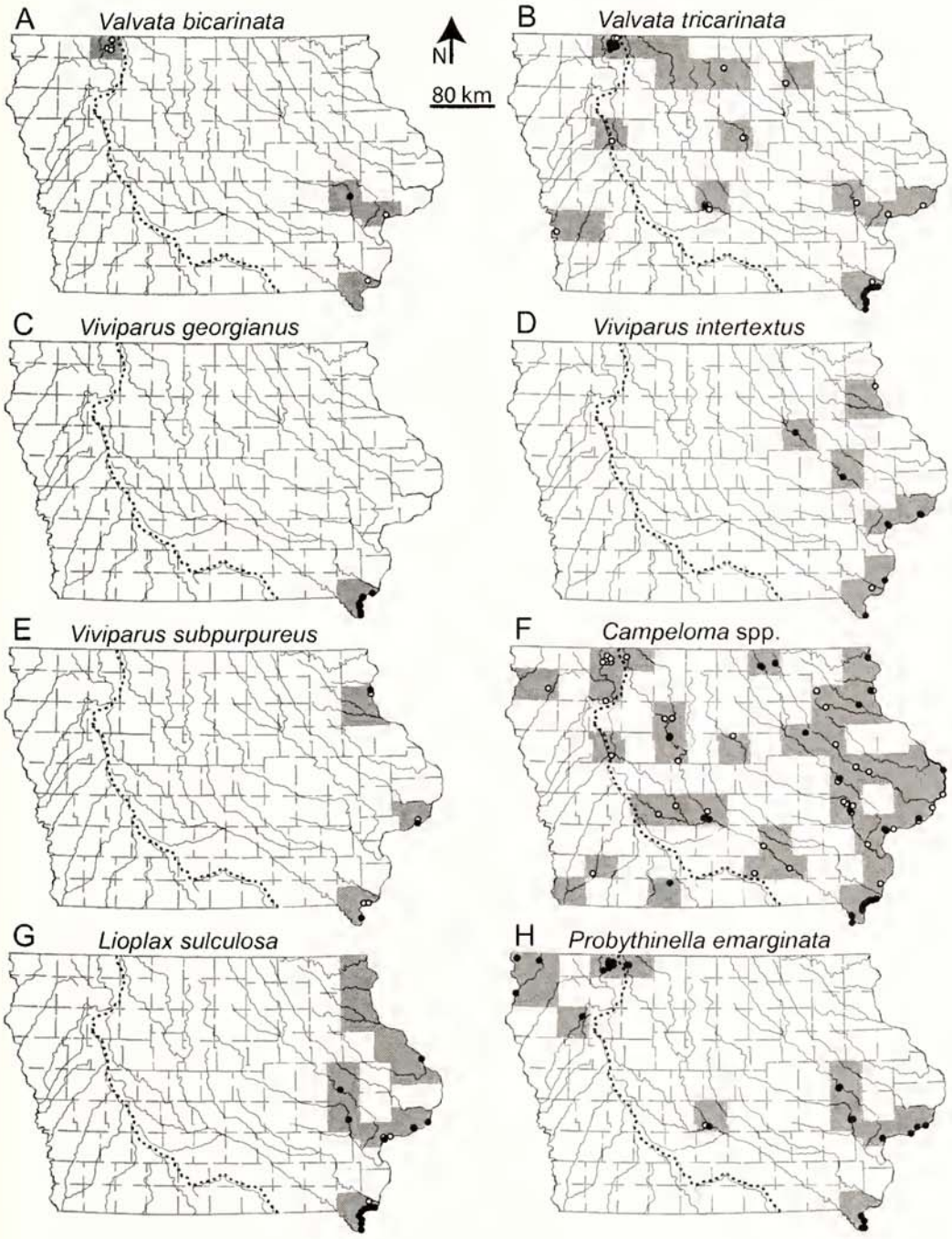

Figure 2. Distributions of (A) *Valvata bicarinata*, (B) *Valvata tricarinata*, (C) *Viviparus georgianus*, (D) *Viviparus intertextus*, (E) *Viviparus subpurpureus*, (F) *Campeloma* spp., (G) *Lioplax sulculosa*, and (H) *Probythinella emarginata* in Iowa. Shading indicates counties where the taxon has been found. Specific localities of occurrence, if known, are indicated by symbols. Unfilled circles indicate records collected before 1950. Filled circles represent records collected during or after 1950, or records from an unknown date.

peloma subsolidus, *Melantho decisa*, *Melantho integra*, *Melantho nolani*, *Melantho ponderosa*, *Melantho subsolida*, *Paludina decisa*, *Paludina integra*, *Paludina ponderosa*, *Paludina regularis*, *Vivipara decisa*, *Vivipara ponderosa*, *Vivipara subsolida*) (Say, 1817). Because of disagreement regarding the number of species in this genus, all *Campeloma* records were mapped together (Shimek 1890, Baker 1928). Individuals of *Campeloma* spp. have been collected from rivers, streams, ponds, and lakes in the Missouri and Mississippi watersheds (Fig. 2F; Haldeman 1840-1845, Tryon 1863, 1865, 1870-1871, Binney 1865a, Pratt 1876, Witter 1878, Call 1880, 1886, 1894, Keyes 1888, Shimek 1890, 1893, 1915, 1935a, Baker 1905, 1928, Van Cleave and Chambers 1935, Carlson 1968, Thompson 1973, Gale 1975, Eckblad *et al.* 1977, BMNH, CMNH, FMNH, NMNH, OSM). Results from surveys of Lake Okoboji suggest that individuals of this genus once occurred in that lake, but were extirpated by 1933 (Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982). However, several recent records exist from elsewhere in Iowa (Carlson 1968, Thompson 1973, Gale 1975, Eckblad *et al.* 1977).

Lioplax sulculosa (Menke, 1827). Although morphologi-

cally similar to *Lioplax subcarinata* (Say, 1816) of the Atlantic drainage in eastern North America, *L. sulculosa* is the only species of *Lioplax* from the Mississippi drainage, and I assigned all records of *Lioplax* to *L. sulculosa* (Clench and Turner 1955). *Lioplax sulculosa* has often been collected from soft substrates in the Mississippi River and nearby tributaries (Fig. 2G; Tryon 1865, Pratt 1876, Witter 1878, Keyes 1888, Van Cleave and Chambers 1935, Clench and Turner 1955, Carlson 1968, Thompson 1973, Gale 1975, Hubert *et al.* 1984, FMNH, OSM).

Family Hydrobiidae

Probythinella emarginata (=*Amnicola binneyana*, *Bithynella obtuse*, *Bythinella obtusa*, *Cincinnatia emarginata*, *Probythinella lacustris*) (Küster, 1852). Individuals of *P. emarginata* have been recorded from ponds, lakes, and rivers in southeastern, central, and northwestern Iowa (Fig. 2H; Witter 1878, Keyes 1888, Shimek 1915, 1935a, Carlson 1968, Bovbjerg *et al.* 1982, Hershler 1996, BMNH, CMC, FMNH). Surveys documented a dramatic decline and recovery of this species in Lake Okoboji during the 20th century. Shimek (1915) first reported it to be common in lakes of the Okoboji region, but it was absent in Lake Okoboji by 1933 (Shimek 1935a). Bovbjerg and Ulmer (1960) also did not find *P. emarginata* in Lake Okoboji from 1954-1959, but Bovbjerg *et al.* (1982) reported it from several locations in that lake in 1979.

Somatogyrus depressus (=*Amnicola depressa*, *Somatogyra depressa*, *Somatogyrus integer*) (Tryon, 1862). This species was first described from snails collected in the Mississippi River at Davenport, Iowa (Tryon 1863). In Iowa, *S. depressus* has been collected from streams and rivers in both Missouri and Mississippi River watersheds (Fig. 3A; Tryon 1863, 1865, 1870-1871, Binney 1865a, Stimpson 1865, Pratt 1876, Keyes 1888, Shimek 1890, 1915, Baker 1928, Carlson 1968, Thompson 1984, Burch 1989, BMNH, CMNH, CMP, DMNH, FMNH, NCM, NMNH).

Birgella subglobosus (=*Birgella subglobosa*, *Somatogyra isogona*, *Somatogyrus isogonus*, *Somatogyrus subglobosus*) (Say, 1825). Individuals of *B. subglobosus* were reported from standing and slow-flowing waters of the Mississippi watershed, including the Mississippi River in southern Iowa, tributaries, and nearby ponds (Fig. 3B; Tryon 1865, Pratt 1876, Witter 1878, Carlson 1968, Thompson 1973, 1984, Gale 1975, BMNH, CMP, FMNH).

Cincinnatia integra (=*Amnicola cincinnatiensis*, *Cincinnatia cincinnatiensis*, *Cincinnatia judayi*) (Say, 1821). The species *C. integra* has a broad historical distribution in Iowa, and is known from ponds, lakes, and rivers in Missouri and Mississippi watersheds (Fig. 3C; Tryon 1865, Pratt 1876, Witter 1878, Keyes 1888, Shimek 1915, 1935a, Hershler and Thompson 1996, BMNH, CMP, FMNH). *Cincinnatia integra* is another species that suffered population declines in Lake Okoboji in the early 20th century. Shimek (1915) considered it to be common in lakes and ponds of the Okoboji region in 1913, but Shimek (1935a), Bovbjerg and Ulmer (1960), and Bovbjerg *et al.* (1982) did not observe individuals of *C. integra* in subsequent surveys of Lake Okoboji. Additional records exist from Lake Okoboji, but dates of these records are unknown (Hershler and Thompson 1996, FMNH).

Pyrgulopsis lustrica (=*Amnicola lustrica*, *Marstonia lustrica*) (Pilsbry, 1890). The species *P. lustrica* has been reported from the Mississippi River in southeastern Iowa and from lakes, streams, and ponds of the Okoboji region in Dickinson County, northwestern Iowa (Fig. 3D; Shimek 1935a, Bovbjerg and Ulmer 1960, Gale 1975, Thompson 1977, Bovbjerg *et al.* 1982, FMNH, NMNH). Shimek (1935a) did not find individuals of *P. lustrica* in his 1933-1934 survey of Lake Okoboji, but stated that the species formerly occurred there. However, *P. lustrica* apparently recovered and was found at several locations in Lake Okoboji in 1954-1959 and 1979 (Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Amnicola limosus (=*Amnicola limosa*, *Amnicola orbiculata*, *Amnicola pallida*, *Amnicola parva*, *Amnicola porata*) (Say, 1817). The species *A. limosus* is known from rivers, ponds, and lakes in northern, central, and southeastern Iowa (Fig. 3E; Pratt 1876, Witter 1878, Keyes 1888, Pilsbry 1898, Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Clampitt 1960, Bovbjerg *et al.* 1982, BMNH, CMNH, CMP, FMNH, NCM). This species also suffered declines and possible extinction in Lake Okoboji early in the 20th century, but was again abundant there in 1979 (Shimek 1915, 1935a, Bovbjerg *et al.* 1982).

Family Pomatiopsidae

Pomatiopsis cincinnatiensis (=*Amnicola sayana*) (Lea, 1840). The species *P. cincinnatiensis* has been reported from four counties in Iowa (Fig. 3F; Tryon 1865, Pratt 1876, Shimek 1915, van der Schalie and Dundee 1955, Gale 1975, Burch and Van Devender 1980). However, records from two counties are questionable. This species is described as semiaquatic; its habitat consists of moist riverbanks (Baker 1928). Although Baker (1928) considered *P. cincinnatiensis* and *A. sayana* to be synonyms, reports of *A. sayana* from the Mississippi River in Lee County in southeastern Iowa and from lakes and ponds of Dickinson County in northwestern Iowa are inconsistent with the habitat requirements of *P. cincinnatiensis* (Shimek 1915, Baker 1928, Gale 1975).

Pomatiopsis lapidaria (Say, 1817). The species *P. lapidaria* is also semiaquatic (van der Schalie and Dundee 1955). It has been reported from moist habitats adjacent to several rivers, but few reports are recent (Fig. 3G; Tryon 1865, Pratt

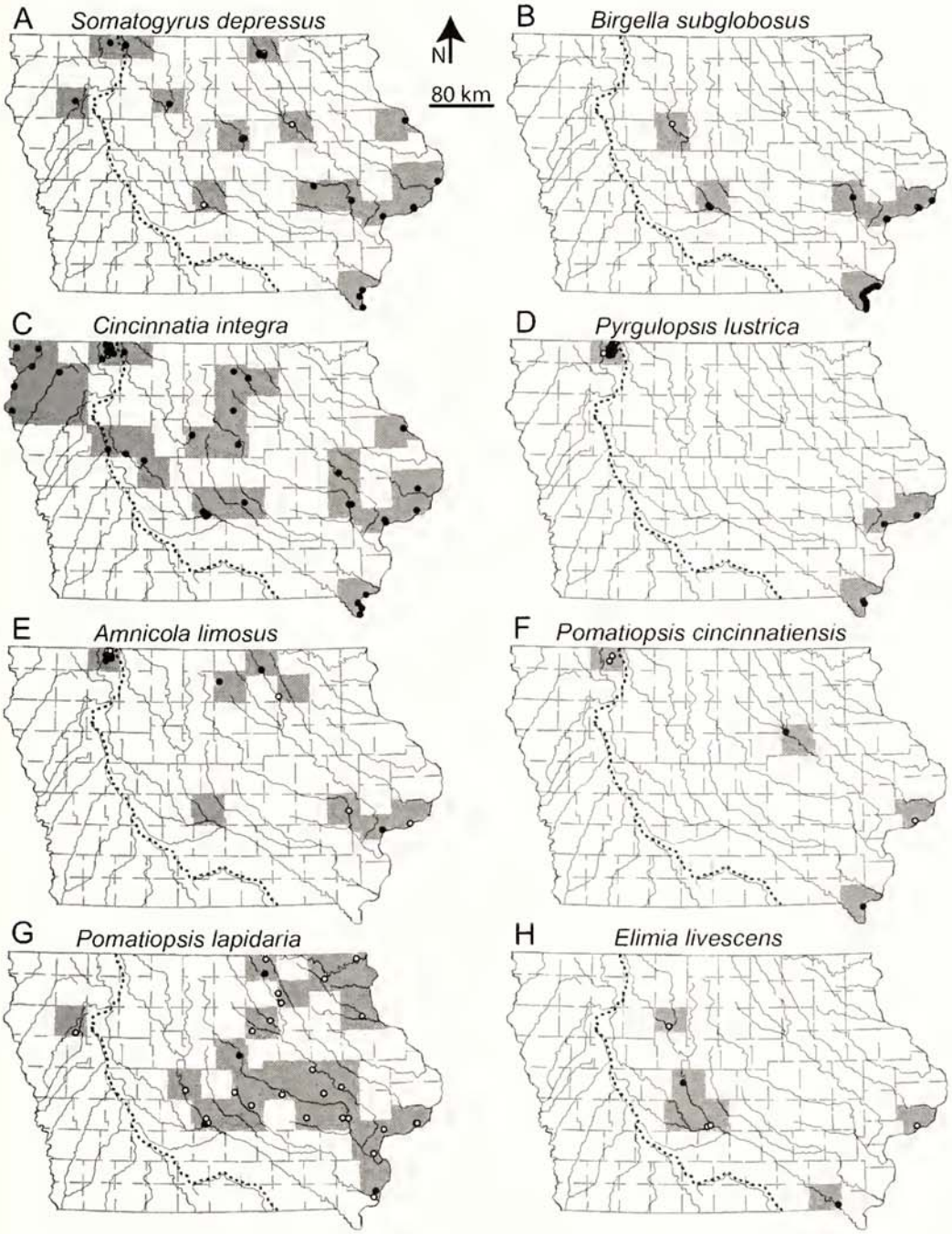

Figure 3. Distributions of (A) *Somatogyrus depressus*, (B) *Birgella subglobosus*, (C) *Cincinnatia integra*, (D) *Pyrgulopsis lustrica*, (E) *Amnicola limosus*, (F) *Pomatiopsis cincinnatiensis*, (G) *Pomatiopsis lapidaria*, and (H) *Elimia livescens* in Iowa. Shading indicates counties where the taxon has been found. Specific localities of occurrence, if known, are indicated by symbols. Unfilled circles indicate records collected before 1950. Filled circles represent records collected during or after 1950, or records from an unknown date.

1876, Pilsbry 1886, Keyes 1888, Shimek 1890, Abbott 1948, Dundee 1957, BMNH, FMNH).

Family Pleuroceridae

Elimia livescens (=*Goniobasis cubicoides*, *Goniobasis cubucoides*, *Goniobasis livescens*) (Menke, 1830). The species *E. livescens* was not often reported, but is known from permanent streams and rivers of the Mississippi watershed (Fig. 3H; Tryon 1865, Pratt 1876, Call 1882, Keyes 1888, Shimek 1893, Dazo 1965, FMNH). This species occurs in habitats dominated by rocks or sand (Dazo 1965).

Pleurocera acuta (=*Pleurocera subulare*, *Trypanostoma subulare*) (Rafinesque, 1831). This species was reported from several rivers in the Mississippi watershed (Fig. 4A; Tryon 1865, Pratt 1876, Witter 1878, Call 1882, Simpson 1895, Dazo 1965, Carlson 1968, Thompson 1973, Gale 1975, BMNH, CMNH, FMNH, INHS, MPM, OSM). Individuals of *P. acuta* occur most frequently in shallow areas of large rivers (Dazo 1965).

Family Lymnaeidae

Acella haldemani (Binney, 1867). Baker (1911) included

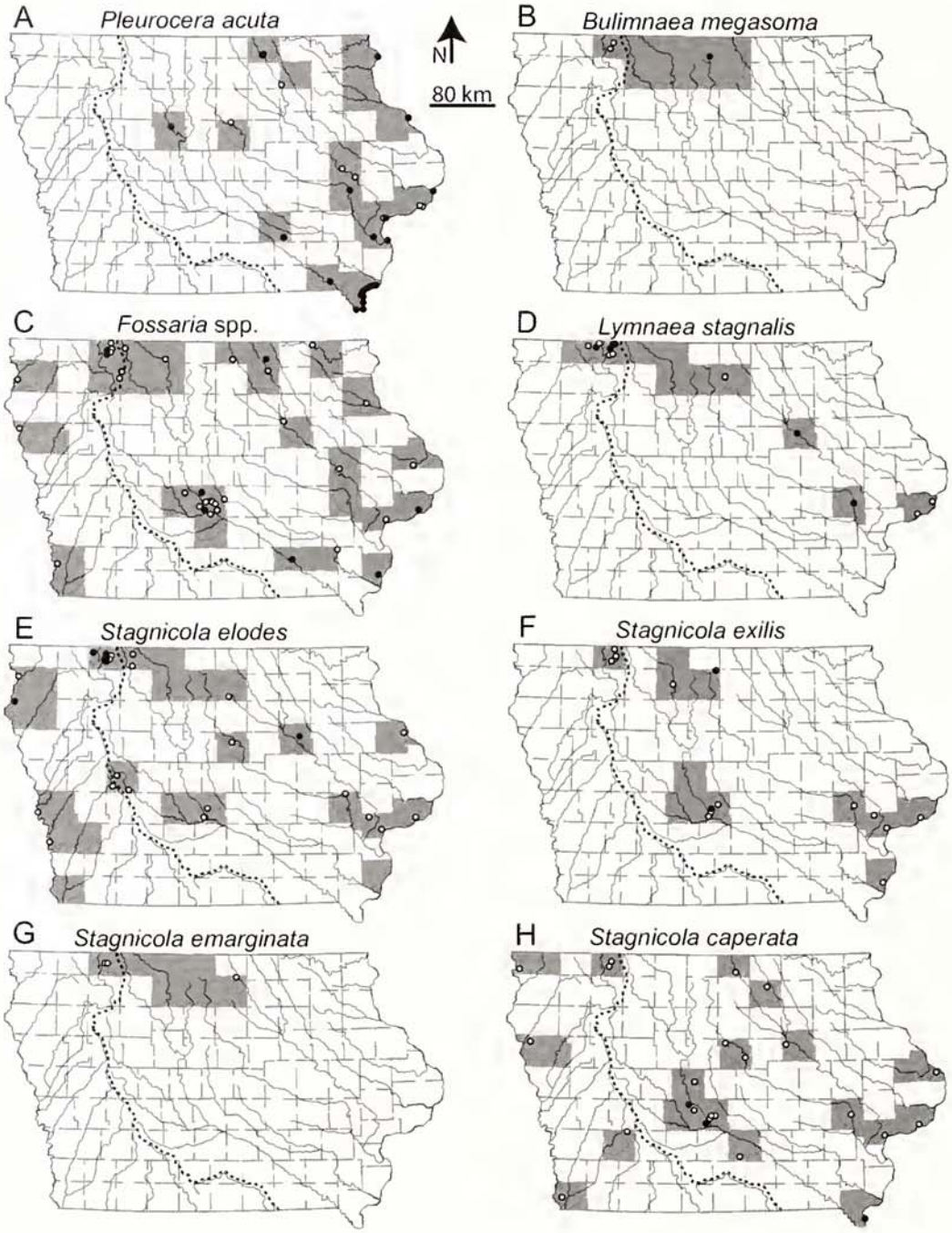

Figure 4. Distributions of (A) *Pleurocera acuta*, (B) *Bulimnaea megasoma*, (C) *Fossaria* spp., (D) *Lymnaea stagnalis*, (E) *Stagnicola elodes*, (F) *Stagnicola exilis*, (G) *Stagnicola emarginata*, and (H) *Stagnicola caperata* in Iowa. Shading indicates counties where the taxon has been found. Specific localities of occurrence, if known, are indicated by symbols. Unfilled circles indicate records collected before 1950. Filled circles represent records collected during or after 1950, or records from an unknown date.

northeastern Iowa as part of the geographic range for *A. haldemani*. However, I found no specific locality records for this species in the state.

Bulimnaea megasoma (=*Bulimnea megasoma*, *Limnaea megasoma*, *Lymnaea megasoma*) (Say, 1824). The species *B. megasoma* was once abundant in lakes and large ponds of northwestern and northcentral Iowa, but an undated report from Winnebago County in northcentral Iowa is the only record that might be recent (Fig. 4B; Keyes 1888, Baker 1911, Shimek 1915, DMNH). Shimek (1915) considered this species to be extinct in the Lake Okoboji region by the early 20th century.

Fossaria spp. (=*Fossaria bulimoides*, *Fossaria exigua*, *Fossaria humilis*, *Fossaria modicella*, *Fossaria obrussa*, *Fossaria parva*, *Galba bulimoides*, *Galba dalli*, *Galba galbana*, *Galba humilis*, *Galba obrussa*, *Galba pallida*, *Galba parva*, *Limnaea decidiosa*, *Limnaea desidiosa*, *Limnaea humilis*, *Limnophysa desidiosa*, *Limnophysa humilis*, *Limnophysa pallida*, *Lymnaea dalli*, *Lymnaea humilis*, *Lymnaea modicella*, *Lymnaea obrussa*, *Lymnaea pallida*, *Lymnaea parva*) (Say, 1822). Taxonomy of the genus *Fossaria* is in a confused state, with species distinguished by minor differences in shell attributes that might be ecophenotypic in origin (Stewart and Dillon 2004). For this reason, I mapped all records of the genus together. This

semiaquatic taxon was collected from exposed mud or shallow submerged areas of ponds, lakes, rivers, and streams throughout Iowa (Fig. 4C; Pratt 1876, Witter 1878, Call 1880, Keyes 1888, Shimek 1890, 1915, Baker 1911, 1928, Bovbjerg and Ulmer 1960, Clampitt 1960, Bovbjerg *et al.* 1982, Coleman 1984, CMNH, CMP, DMNH, FMNH, NCM). The genus *Fossaria* declined in abundance in Lake Okoboji in the early 20th century, but later increased in abundance following improvements in water quality (Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Lymnaea stagnalis (=*Limnaea stagnalis*) (Linnaeus, 1758). The species *L. stagnalis* has been recorded from lakes, ponds, and swamps in northern and eastern Iowa (Fig. 4D; Tryon 1865, Keyes 1888, Baker 1911, Shimek 1915, 1935a, Bovbjerg 1968, Brown 1979a, 1979b, 1983, Coleman 1984, Kessel and Beams 1984, DMNH, FMNH). Keyes (1888) and Shimek (1890) considered *L. stagnalis* to be abundant in northern Iowa. However, Shimek (1915) later remarked that it was no longer common in Lake Okoboji or elsewhere in the region, and neither Shimek (1935a), Bovbjerg and Ulmer (1960), or Bovbjerg *et al.* (1982) reported this species in subsequent surveys of Lake Okoboji. Shimek (1935a) also recognized dramatic declines in abundance of *L. stagnalis* in the entire region of northern Iowa between Spirit Lake in Dickinson County and Clear Lake in Cerro Gordo County. However, recent records suggest this species persisted in wetlands of northern Iowa at the end of the 20th century (Bovbjerg 1968, Brown 1979a, 1979b, 1983, Coleman 1984).

Stagnicola elodes (=*Galba elodes*, *Galba iowaensis*, *Galba palustris*, *Galba reflexa*, *Galba umbrosa*, *Limnaea palustris*, *Limnaea reflexa*, *Limnaea umbrosa*, *Limnaeus elodes*, *Limnea umbrosa*, *Limneus elongatus*, *Limnophysa nuttaliana*, *Limnophysa palustris*, *Limnophysa reflexa*, *Limnophysa umbrosa*, *Lymnaea elodes*, *Lymnaea palustris*, *Lymnaea reflexa*, *Lymneus elongatus*, *Lymneus umbrosus*, *Stagnicola crystallensis*, *Stagnicola palustris*, *Stagnicola reflexa*, *Stagnicola umbrosa*) (Say, 1821). The species *S. elodes* has been recorded from ephemeral and permanent ponds and swamps and from embayments of lakes throughout Iowa (Fig. 4E; Say 1832, Haldeman 1840-1845, Tryon 1865, Pratt 1876, Witter 1878, Call 1880, Keyes 1888, Baker 1904, 1911, 1928, Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Bovbjerg 1965, 1968, Brown 1979a, Bovbjerg *et al.* 1982, Coleman 1984, CAS, DMNH, FMNH). Although Shimek (1915, 1935a) reported severe reductions in the abundance of *S. elodes* in Lake Okoboji and northern Iowa generally, populations in Lake Okoboji later recovered (Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Stagnicola exilis (=*Galba exilis*, *Galba kirtlandiana*, *Limnaea zebra*, *Limnophysa zebra*, *Lymnaea exilis*, *Lymnaea zebra*) (Lea, 1834). Historically, the species *S. exilis* occurred in ephemeral and permanent lentic habitats in northern, central, and southeastern Iowa, but few recent records exist (Fig. 4F; Tryon 1865, Keyes 1888, Baker 1911, Shimek 1915, Bovbjerg 1968, FMNH). It has not been reported from Lake Okoboji since 90 years ago, when Shimek (1915) noted that *S. exilis* was widely distributed but uncommon.

Stagnicola catascopium (=*Galba catascopium*, *Lymnaea catascopium*) (Say, 1867). The only records I found for *S. catascopium* were from northern Iowa in the vicinities of Ruthven and Charles City, in Palo Alto and Floyd counties, respectively (Baker 1911).

Stagnicola emarginata (=*Galba emarginata*, *Lymnaea emarginata*) (Say, 1821). Historically, individuals of *S. emarginata* inhabited the kettlehole region of northern Iowa, encompassing the area between Lake Okoboji in Dickinson County and Clear Lake in Cerro Gordo County (Fig. 4G; Baker 1911, Shimek 1915, Shimek 1935a). Shimek (1935a) remarked that *S. emarginata* was once abundant in the kettlehole region but had vanished by 1933. This species has not been reported from Iowa in more than 90 years.

Stagnicola caperata (=*Galba caperata*, *Limnaea caperata*, *Limnophysa caperata*, *Lymnaea caperata*, *Lymnaea umbilicata*) (Say, 1829). The species *S. caperata* has been reported from marshes, swamps, vernal ponds, and lake margins throughout Iowa, but few observations were made of this wetland species in recent years (Fig. 4H; Pratt 1876, Witter 1878, Keyes 1888, Baker 1911, Shimek 1915, FMNH).

Family Physidae

Physa skinneri (Taylor, 1954). Burch (1989) considered Iowa to be within the geographic range of *P. skinneri*, but I did not find records confirming this. The species occurs in prairie pothole wetlands of the Dakotas and might exist in similar habitats of northwestern Iowa (Euliss *et al.* 1999).

Physella gyrina (=*Physella ancillaria*, *Physella elliptica*, *Physella hildrethiana*, *Physella lordi*, *Physella oleacea*, *Physella sayi*, *Physella sayii*) (Say, 1821). Results from breeding experiments recently revealed a lack of reproductive isolation among several nominal species of *Physella* (=*Physa*), resulting in *Physella ancillaria* (Say, 1825) and *Physella gyrina* being synonymized (Dillon and Wethington 2004). *Physella gyrina* was originally described by Say (1821) from a population located in southwestern Iowa near Council Bluffs, in Pottawattamie County. It has since been found in almost any habitat supporting freshwater snails (Fig. 5A; Say 1821, Haldeman 1840-1845, Binney 1865b, Tryon 1865, Pratt 1876, Witter 1878, Call 1880, Keyes 1888, Shimek 1890, 1915, 1935a, Baker 1905, 1928, Wurtz 1949, Ulmer and Sommer 1957, Bovbjerg and Ulmer 1960, Clampitt 1960, 1970, Ulmer 1960, Bovbjerg *et al.* 1970, Rausch and Bovbjerg 1973, Gale 1975, Te 1975, Brown 1979a, Bovbjerg *et al.* 1982, Coleman 1984, Dillon and Wethington 2004, CMNH, DMNH,

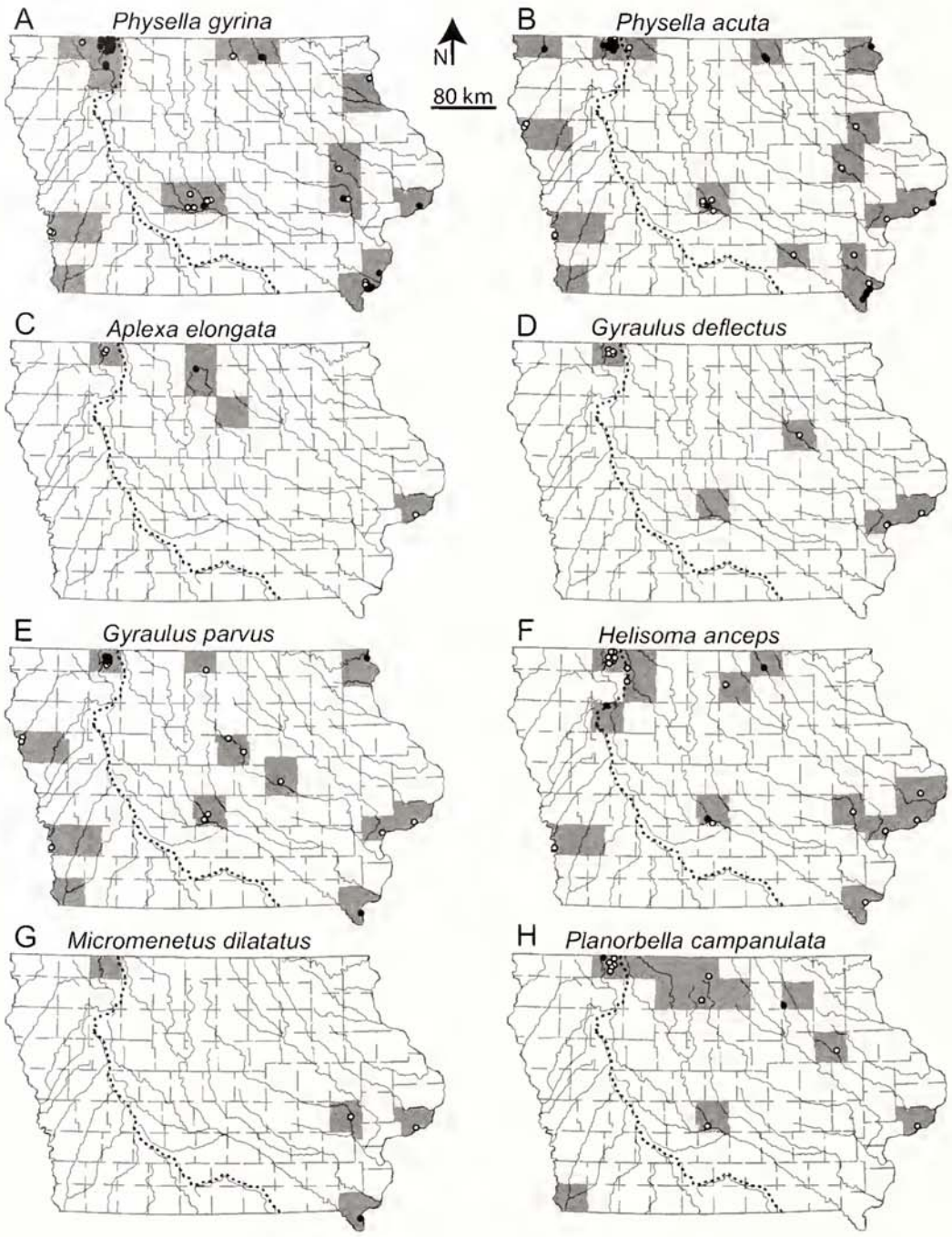

Figure 5. Distributions of (A) *Physella gyrina*, (B) *Physella acuta*, (C) *Aplexa elongata*, (D) *Gyraulus deflectus*, (E) *Gyraulus parvus*, (F) *Helisoma anceps*, (G) *Micromenetus dilatatus*, and (H) *Planorbella campanulata* in Iowa. Shading indicates counties where the taxon has been found. Specific localities of occurrence, if known, are indicated by symbols. Unfilled circles indicate records collected before 1950. Filled circles represent records collected during or after 1950, or records from an unknown date.

FMNH, INHS, MPM, OSM). Similar to other species of gastropods, *P. gyrina* was nearly if not completely extirpated from Lake Okoboji in the early 20th century (Shimek 1915, 1935a). However, *P. gyrina* was very abundant in 1954-1959 and 1979 surveys of Lake Okoboji (Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Physella acuta (=*Physella anatina*; *Physella halei*, *Physella heterostropha*, *Physella integra*, *Physella virgata*, *Physella walkeri*) (Draparnaud, 1805). After finding no evidence of reproductive isolation among several species of *Physella* (=*Physa*) reported from Iowa, including *P. acuta*, *Physella heterostropha* (Say, 1817), *Physella integra* (Haldeman, 1841), and *Physella virgata* (Gould, 1855), Dillon *et al.* (2002) assigned the name *Physella acuta* to this entire group. *Physella acuta* has been recorded from almost every freshwater habitat in Iowa (Fig. 5B; Say 1821, Tryon 1865, Pratt 1876, Witter 1878, Call 1880, Keyes 1888, Shimek 1890, 1915, 1935a, Walker 1918, Bovbjerg and Ulmer 1960, Clampitt 1970, Gale 1975, Eckblad *et al.* 1977, Brown 1979a, Bovbjerg *et al.* 1982, Coleman 1984, CMNH, CMP, DMNH, FMNH, OSM). This is one of the most pollution-tolerant freshwater snails, yet even it declined in abundance in Lake Okoboji during the early 20th century (Shimek 1915, 1935a). A few individuals of *P. acuta* were the only gastropods of any kind found in

Lake Okoboji during a 1933-1934 survey (Shimek 1935a). By 1979, this species was again abundant in that lake (Bovbjerg *et al.* 1982).

Aplexa elongata (=*Aplexa hypnorum*) (Say, 1821). Individuals of the species *A. elongata* have been collected from ponds and slow-moving streams in northern and southeastern Iowa (Fig. 5C; Tryon 1865, Pratt 1876, Keyes 1888, Shimek 1890, 1915, Coleman 1984, FMNH). Several malacologists remarked that *A. elongata* was abundant and widely distributed in northern Iowa in the 19th and early 20th centuries (Pratt 1876, Keyes 1888, Shimek 1890, 1915). Shimek (1915) reported *A. elongata* from Lake Okoboji, but it was not found in several subsequent surveys of that lake conducted from 1933-1979 (Shimek 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982). The scarcity of recent records suggests this species also suffered other local extinctions. However, a recent record from an unspecified location in Dickinson County suggests *A. elongata* still inhabited Iowa near the end of the 20th century (Coleman 1984). An undated record also occurs from Crystal Lake in Hancock County (FMNH).

Family Planorbidae

Gyraulus deflectus (=*Gyraulus hirsutus*, *Planorbis deflectus*) (Say, 1824). Individuals of *G. deflectus* were collected from several swamps, ponds, and lakes, but this species has not been reported from Iowa in almost 60 years (Fig. 5D; Tryon 1865, Pratt 1876, Witter 1878, Keyes 1888, Shimek 1915, 1935a, Baker 1945, FMNH). This species once occurred in shallow areas of Lake Okoboji, but was absent in 1933 and had not returned as of 1979 (Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Gyraulus circumstriatus (Tryon, 1866). An undated report of *G. circumstriatus* from Des Moines in Polk County constitutes the only known record of this species in Iowa (FMNH).

Gyraulus parvus (=*Planorbis parvus*) (Say, 1817). Individuals of *G. parvus* have been found in ponds, swamps, lakes, and slow-flowing vegetated areas of rivers throughout Iowa (Fig. 5E; Say 1821, Tryon 1865, Pratt 1876, Witter 1878, Call 1880, Keyes 1888, Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Clampitt 1960, Eckblad *et al.* 1977, Bovbjerg *et al.* 1982, Coleman 1984, FMNH). Following a decline in Lake Okoboji in the early 1900s, this species recovered rapidly and was one of the most abundant snails in that lake by 1979 (Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Clampitt 1960, Bovbjerg *et al.* 1982).

Helisoma anceps (=*Helisoma antrosa*, *Helisoma antrosum*, *Helisoma bicarinatus*, *Planorbis antrosus*, *Planorbis bicarinatus*) (Menke, 1830). This species has been collected from a wide range of habitats throughout Iowa, including ponds, lakes, and rivers (Fig. 5F; Say 1821, Tryon 1865, Pratt 1876, Witter 1878, Keyes 1888, Walker 1909, Shimek 1915, 1935a, Baker 1945, Meierhoff and Prill 1982, Kennedy and Miller 1990, CMNH, DMNH, FMNH, NCM, NMNH). Although recent records exist for *H. anceps* in Iowa, this species apparently disappeared from Lake Okoboji by 1933, and was not observed during subsequent surveys of that lake (Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Micromenetus dilatatus (=*Menetus dilatatus*, *Planorbis dilatatus*) (Gould, 1841). Individuals of *M. dilatatus* have occasionally been collected from lagoons and shallow regions of lakes in Iowa (Fig. 5G; Shimek 1890, 1915, FMNH). A 1969 record from Montrose in Lee County is the only recent record for this species in the state (FMNH).

Planorbella campanulata (=*Helisoma campanulata*, *Helisoma campanulatum*, *Planorbella campanulatum*, *Planorbella campanulatus*, *Planorbis campanulatus*) (Say, 1821). The species *P. campanulata* has been recorded from ponds, lakes, and rivers of the Mississippi and Missouri watersheds (Fig. 5H; Binney 1865b, Tryon 1865, Call 1880, Keyes 1888, Shimek 1915, 1935a, Bovbjerg *et al.* 1970, FMNH). *Planorbella campanulata* was once reported to be common in lakes of northern Iowa (Keyes 1888). Shimek (1915) later remarked that the species was present but uncommon in shallow regions of Lake Okoboji and the Gar lakes in Dickinson County. Individuals of *P. campanulata* were not encountered in more recent surveys of Lake Okoboji (Shimek 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Planorbella trivolvis (=*Helisoma regularis*, *Helisoma trivolvis*, *Pierosoma trivolvis*, *Planorbis binneyi*, *Planorbis lentus*, *Planorbis trivolvis*) (Say, 1817). This widely distributed species was reported from ponds, wetlands, and quiet areas of rivers (Fig. 6A; Say 1821, Say 1834 in Binney 1858, Binney 1865b, Tryon 1865, Pratt 1876, Witter 1878, Call 1880, Keyes 1888, Shimek 1915, Bovbjerg and Ulmer 1960, Kater and Koneko 1972, Gale 1975, Bovbjerg *et al.* 1982, Coleman 1984, CMNH, DMNH, FMNH, INHS, NMNH, OSM, SBM). *Planorbella trivolvis* was abundant in shallow and swampy areas of Lake Okoboji in the early 20th century, but was not found in a 1933-1934 survey of that lake (Shimek 1915, 1935a). The species was uncommon but present in subsequent surveys of Lake Okoboji (Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Planorbella truncata (=*Helisoma truncata*; *Helisoma truncatum*, *Planorbella truncatum*, *Planorbis truncatus*) (Miles, 1861). Individuals of *P. truncata* were recorded from lakes in northern Iowa as late as 1945, but have not been seen anywhere since (Fig. 6B; Shimek 1915, 1935a, Baker 1945, DMNH). Shimek (1915) was the last to report it from Lake Okoboji and the Gar lakes of Dickinson County. Shimek (1935a) also reported *P. truncata* from the kettlehole region between Spirit and Clear lakes in Dickinson and

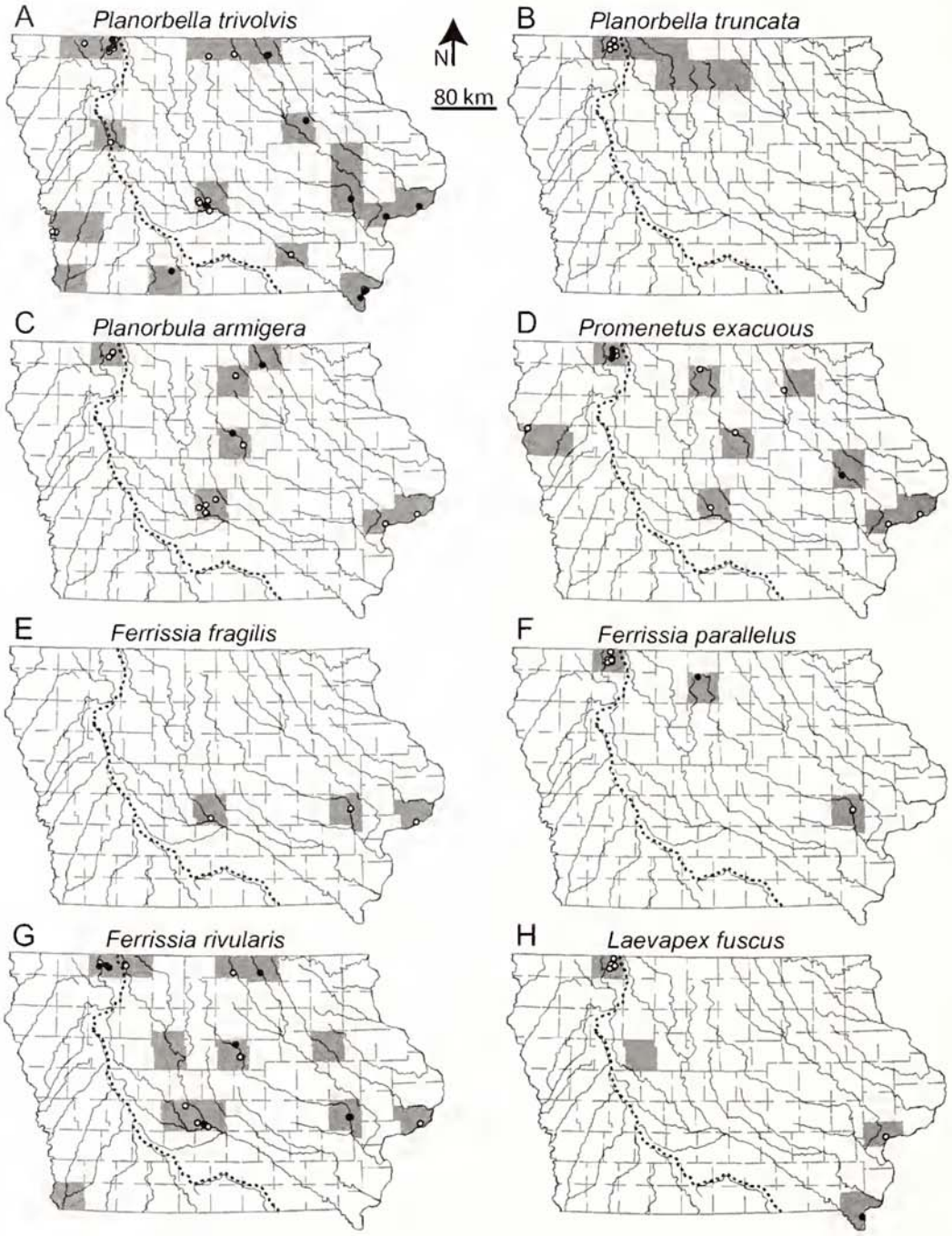

Figure 6. Distributions of (A) *Planorbella trivolvis*, (B) *Planorbella truncata*, (C) *Planorbula armigera*, (D) *Promenetus exacuous*, (E) *Ferrissia fragilis*, (F) *Ferrissia parallelus*, (G) *Ferrissia rivularis*, and (H) *Laevapex fuscus* in Iowa. Shading indicates counties where the taxon has been found. Specific localities of occurrence, if known, are indicated by symbols. Unfilled circles indicate records collected before 1950. Filled circles represent records collected during or after 1950, or records from an unknown date.

Cerro Gordo counties, but remarked that its numbers were much reduced relative to earlier surveys.

Planorbula armigera (=*Planorbella armigera*, *Planorbis armigera*, *Planorbis armigerus*, *Planorbula jenksii*, *Segmentina armigera*, *Segmentina wheatleyi*) (Say, 1821). Individuals of *P. armigera* were reported from several wetlands, lakes, and rivers (Fig. 6C; Tryon 1865, Pratt 1876, Witter 1878, Keyes 1888, Shimek 1915, Baker 1945, CMNH, CMP, DMNH, FMNH). This species was present in shallow regions of Lake Okoboji before 1915, but was not found in later surveys of the lake (Shimek 1915, 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982). The most recent known sighting in Iowa of *P. armigera* occurred in 1942, although some undated records could be more recent (CMNH, DMNH, FMNH).

Promenetus exacuous (=*Menetus exacuous*, *Menetus exacutus*, *Planorbis exacutus*) (Say, 1821). The species *P. exacuous* has been reported from ponds, lakes, and quiet areas of rivers (Fig. 6D; Tryon 1865, Pratt 1876, Witter 1878, Shimek 1915, 1935a, Baker 1945, Bovbjerg and Ulmer 1960, Clampitt 1960, Bovbjerg *et al.* 1982, Coleman 1984, DMNH, FMNH). Shimek (1915) found individuals of *P. exacuous* in shallow waters of the Lake Okoboji region of Dickinson County in northwestern Iowa. Although he did not report it

from his 1933-1934 survey of Lake Okoboji, it was present at several locations in that lake during 1954-1959 and 1979 surveys (Shimek 1935a, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982).

Promenetus umbilicatellus (=*Gyraulus umbilicatelus*) (Cockerell, 1887). Baker (1945) reported this species from an unspecified location in Iowa. I found no additional records for *P. umbilicatellus*.

Family Ancylidae

Ferrissia fragilis (=*Ancylus pumilus*, *Ferrissia shimekii*, *Gundlachia meekiana*) (Tryon, 1863). Individuals of *F. fragilis* were reported from central and eastern Iowa (Fig. 6E; Pilsbry 1886, Walker 1904, FMNH). This species has not been reported from Iowa since 1912 (FMNH). However, this tiny gastropod is easily overlooked and difficult to distinguish from *Ferrissia rivularis* (Say 1817). *Ferrissia fragilis* is tolerant of organic pollution and might still survive in eutrophic, vegetated wetlands and lakes in Iowa (Basch 1963).

Ferrissia parallelus (=*Ancylus parallelus*, *Ferrissia parallela*) (Haldeman, 1841). *Ferrissia parallelus* was recorded in the 1800s and early 1900s from several lakes in northwestern Iowa, and from a single location in Iowa City, Johnson County (Fig. 6F; Shimek 1890, 1915, 1935a, 1935b, Walker, 1904, FMNH). Shimek (1915) considered this species to be extinct in the Lake Okoboji region of northwestern Iowa by the early 20th century, and with the possible exception of an undated record from Crystal Lake, Hancock County, *F. parallelus* has not been reported from Iowa in more than 80 years (FMNH).

Ferrissia rivularis (=*Ancylus rivularis*, *Ancylus tardus*, *Ferrissia tarda*, *Ferrissia tardus*) (Say, 1817). The species *F. rivularis* is the most frequently reported ancylid in Iowa (Fig. 6G; Tryon 1865, Pratt 1876, Call 1880, Keyes 1888, Shimek 1915, 1935b, Bovbjerg and Ulmer 1960, Bovbjerg *et al.* 1982, CMNH, FMNH). *Ferrissia rivularis* is considered to be restricted to streams, rivers, and lakes with strong current or wave action (Baker 1928, Basch 1963). Bovbjerg and Ulmer (1960) and Bovbjerg *et al.* (1982) reported this species from a protected bay in Lake Okoboji, but this area is more consistent with the habitat of *Ferrissia fragilis*, a taxon that is morphologically similar to *F. rivularis* (Basch 1963, Burch 1989).

Laevapex diaphanus (=*Ancylus diaphanus*) (Haldeman, 1841). I found two records for *L. diaphanus*, including one from eastern Iowa and one from northwestern Iowa. Specimens were collected from a pond near Iowa City, Johnson County, on an unknown date and from shallow standing waters of the Lake Okoboji region in Dickinson County in the late 1800s and early 1900s (Shimek 1915, FMNH).

Laevapex fuscus (=*Ancylus fuscus*, *Ferrissia fusca*, *Ferrissia kirtlandi*) (Adams, 1841). The species *L. fuscus* has been reported from wetlands, lakes, and rivers in Iowa (Fig. 6H; Witter 1878, Shimek 1935a, 1935b, Gale 1975, FMNH). It was apparently extirpated from Lake Okoboji before 1933, but persisted long after that time in southeastern Iowa (Shimek 1935a, Gale 1975).

DISCUSSION

Iowa historically supported at least 49 species of freshwater gastropods, including 47 taxa recognized as true species and two genera consisting of an undetermined number of species. This diversity compares favorably to taxonomic richnesses in other recently surveyed states that are smaller or similar in size to Iowa, including Connecticut (35 species; Jokinen 1983), Maine (45 species; Martin 1999), New York (61 species; Jokinen 1992), and Virginia (53 species; Stewart and Dillon 2004). Abundant and diverse aquatic habitats enabled relatively high freshwater gastropod diversity in Iowa. An impressive variety of "prosobranchs" (e.g., Viviparidae, Hydrobiidae, and Pleuroceridae) has been recorded from the eastern portion of the Mississippi River watershed. Probable explanations for this rich assemblage include emigrations from the Great Lakes via the Mississippi River and diverse benthic habitats in the abundant rivers of the region (Dazo 1965). Additionally, a very different yet diverse group of "pulmonates" (e.g., Lymnaeidae, Planorbidae) is known from the prairie pothole and kettlehole region of northcentral and northwestern Iowa, where abundant ephemeral and permanent lentic habitats occur (Prior 1991). In contrast, few gastropod taxa have been recorded from southwestern Iowa. Although it appears that little effort has been directed to sampling gastropods of southwestern Iowa, sediments of the loess soils ecoregion that dominate this area readily erode, resulting in streams with heavy silt loads and muddy beds that are inhospitable to most gastropods (Prior 1991).

Lack of attention to freshwater gastropods might also explain the absence or rarity of recent records for some snail taxa. However, surveys from northern Iowa provide strong evidence that gastropod abundance and diversity declined in that region from the beginning to the end of the 20th century. In 1954-1959 and 1979, Bovbjerg and Ulmer (1960) and Bovbjerg *et al.* (1982) found 11 and 12 species of gastropods in Lake Okoboji, respectively. Although diversity in those studies was substantially higher than in 1933-1934, when only one species was recovered, it remained far below the 32 species reported from Lake Okoboji at the beginning of the 20th century (Shimek 1915, 1935a, Bovbjerg *et al.* 1982). Declines in abundance and diversity in the early 20th century were not restricted to Lake Okoboji. Shimek (1935a)

reported declines in the abundance and diversity of freshwater gastropods across the entire kettlehole region of northern Iowa between Spirit Lake, Dickinson County, and Clear Lake, Cerro Gordo County. Severe pollution of rivers and lakes and destruction of wetland habitat were blamed for declines in gastropod abundance and diversity in northern Iowa in the late 19th and early 20th centuries (Shimek 1935a). Because similar habitat degradation and loss occurred in other regions of Iowa, snail abundance and diversity probably declined throughout much of the state during that time period (Shimek 1935a, Euliss and Mushet 1999). However, increased abundance and diversity of gastropods in Lake Okoboji following improvements in water quality in the latter half of the 20th century indicate that many taxa respond favorably and quickly to abatement of pollution (Bovbjerg *et al.* 1982). If modern strategies to protect water quality are successful, the conservation status of many gastropod taxa should improve (Prior *et al.* 2003). Additionally, snails have likely benefited from recent increases in wetland habitat in Iowa, although gastropod responses to wetland creation and restoration have not yet been evaluated (Bishop *et al.* 1998).

Based on rarity or absence of recent records and evidence of local extinctions associated with pollution and habitat loss, I consider 25 of Iowa's freshwater gastropod taxa to be of conservation concern. Of these taxa, *Valvata lewisi*, *Valvata sincera*, *Acella haldemani*, *Stagnicola catascopium*, *Stagnicola emarginata*, *Planorbella truncata*, and *Planorbella umbillicatellus* probably no longer occur in Iowa. These species have localized historic distributions in the state and have not been reported since 1945 or earlier. *Valvata bicarinata*, *Pomatiopsis cincinnatiensis*, *Pomatiopsis lapidaria*, *Bulimnaea megasoma*, *Physa skinneri*, *Gyraulus deflectus*, *Gyraulus circumstriatus*, *Planorbula armigera*, *Ferrissia fragilis*, *Ferrissia parallelus*, and *Laevapex diaphanus* were rarely reported in recent years, and could also be imperiled or extinct in Iowa. Several additional species likely survive today but were eliminated from many former habitats and appear to be less widespread now than formerly, including *Lymnaea stagnalis*, *Stagnicola exilis*, *Stagnicola caperata*, *Aplexa elongata*, *Micromenetus dilatatus*, *Planorbella campanulata*, and *Laevapex fuscus*.

An objective of this review is to facilitate and stimulate additional research that will improve the conservation status of freshwater gastropods in Iowa and North America in general. A comprehensive field survey of Iowa's freshwater gastropods is needed now to determine which species are truly endangered in this state. Comparisons of data from future field surveys with the historic data I summarized here will provide evidence of restricted or shrinking geographic ranges needed to establish legal protection and recovery action plans for imperiled species.

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LITERATURE CITED

Abbott, R. T. 1948. A potential snail host of oriental schistosomiasis in North America (*Pomatiopsis lapidaria*). *Proceedings of the United States National Museum* **98**: 57-68.

Angelo, R. T., M. S. Cringan, and J. E. Fry. 2002. Distributional revisions and new and amended occurrence records for prosobranch snails in Kansas. *Transactions of the Kansas Academy of Science* **105**: 246-257.

Baker, F. C. 1904. New varieties of American lymnaeas. *The Nautilus* **18**: 10-12.

Baker, F. C. 1905. The molluscan fauna of McGregor, Iowa. *The Nautilus* **15**: 249-258.

Baker, F. C. 1911. *The Lymnaeidae of North and Middle America, Recent and Fossil*. Chicago Academy of Sciences Special Publication No. 3, Chicago, Illinois.

Baker, F. C. 1928. *The Fresh Water Mollusca of Wisconsin*, Part I. Gastropoda. Wisconsin Academy of Sciences, Arts, and Letters, Madison, Wisconsin.

Baker, F. C. 1945. *The Molluscan Family Planorbidae*. The University of Illinois Press. Urbana, Illinois.

Bardach, J. E., J. Morrill, and F. Gambony. 1951. Preliminary report on the distribution of bottom organisms in West Lake Okoboji, Iowa. *The Proceedings of the Iowa Academy of Science* **58**: 405-414.

Barnhart, M. C. 1978. Three introduced gastropods in Iowa. *The Nautilus* **92**: 106-107.

Basch, P. F. 1963. A review of the recent freshwater limpet snails of North America (Mollusca: Pulmonata). *Bulletin of the Museum of Comparative Zoology, Harvard University* **129**: 399-461.

Binney, W. G. 1858. *The Complete Writings of Thomas Say*. H. Bailliere, New York.

Binney, W. G. 1865a. Land and fresh water shells of North America, Part III. Ampullaridae, Valvatidae, Viviparidae, fresh water Rissoidae, Cyclophoridae, Truncatellidae, fresh-water Neritidae, Helicinidae. *Smithsonian Miscellaneous Collections* **144**: i-vii, 1-120.

Binney, W. G. 1865b. Land and fresh water shells of North America, Part II. Pulmonata, Limnophila and Thalassophila. *Smithsonian Miscellaneous Collections* **143**: i-ix, 1-161.

Bishop, R. A., J. Joens, and J. Zohrer. 1998. Iowa's wetlands, present and future with a focus on prairie potholes. *Journal of the Iowa Academy of Science* **105**: 89-93.

Bogan, A. E. 1998. Freshwater molluscan conservation in North

America: Problems and practices. *Journal of Conchology Special Publication* **2**: 223-230.

Bovbjerg, R. V. 1965. Feeding and dispersal in the pond snail *Stagnicola reflexa* (Basommatophora: Lymnaeidae). *Malacologia* **2**: 199-207.

Bovbjerg, R. V. 1968. Responses to food in lymnaeid snails. *Physiological Zoology* **41**: 412-423.

Bovbjerg, R. V. and M. J. Ulmer. 1960. An ecological catalog of the Lake Okoboji gastropods. *The Proceedings of the Iowa Academy of Science* **67**: 569-577.

Bovbjerg, R. V., R. L. Dusil, and R. L. Broer. 1982. The gastropods of Lake West Okoboji, Iowa, twenty years later. *The Proceedings of the Iowa Academy of Science* **89**: 62-67.

Bovbjerg, R. V., N. L. Pearsall, and M. L. Brackin. 1970. A preliminary faunal study of the upper Little Sioux River. *The Proceedings of the Iowa Academy of Science* **77**: 177-184.

Brönmark, C. and J. E. Vermaat. 1998. Complex fish-snail-epiphyton interactions and their effects on submerged freshwater macrophytes. *In*: M. Søndergaard and K. Christoffersen, eds., *The Structuring Role of Submerged Macrophytes in Lakes*. Springer-Verlag, New York. Pp. 47-68.

Brown, K. M. 1979a. The adaptive demography of four freshwater pulmonate snails. *Evolution* **33**: 417-432.

Brown, K. M. 1979b. Effects of experimental manipulations on the life history pattern of *Lymnaea stagnalis appressa* Say (Pulmonata: Lymnaeidae). *Hydrobiologia* **65**: 165-176.

Brown, K. M. 1983. Do life history tactics exist at the intraspecific level? Data from freshwater snails. *American Naturalist* **121**: 871-879.

Brown, K. M. 2001. Mollusca: Gastropoda. *In*: J. H. Thorp and A. P. Covich, eds., *Ecology and Classification of North American Freshwater Invertebrates*, Academic Press, New York. Pp. 297-329.

Burch, J. B. 1989. *North American Freshwater Snails*. Malacological Publications, Hamburg, Michigan.

Burch, J. B. and A. S. Van Devender. 1980. Identification of Eastern North American Land Snails: The Prosobranchia, Opisthobranchia and Pulmonata (Actophila). *Transactions of the POETS Society* **1**: 33-80.

Call, R. E. 1880. Fresh-water mollusks. *In*: Iowa Historical Society, ed., *History of Fremont County, Iowa*, Des Moines, Iowa. Pp. 34-36.

Call, R. E. 1882. Note on the geographical distribution of certain mollusks. *American Naturalist* **16**: 400-402.

Call, R. E. 1886. On the genus *Campeloma*, Rafinesque, with a revision of the species, recent and fossil. *Bulletin of the Washburn College Laboratory of Natural History* **1**: 149-165.

Call, R. E. 1894. On the geographic and hypsometric distribution of North American viviparids. *The American Journal of Science* **48**: 132-141.

Carlson, C. A. 1968. Summer bottom fauna of the Mississippi River, above dam 19, Keokuk, Iowa. *Ecology* **49**: 162-169.

Clampitt, P. T. 1960. An ecological reconnaissance of the bottom fauna, Miller's Bay, Lake Okoboji. *The Proceedings of the Iowa Academy of Science* **67**: 553-567.

Clampitt, P. T. 1970. Comparative ecology of the snails *Physa gyrina* and *Physa integra* (Basommatophora: Physidae). *Malacologia* **10**: 113-151.

Clench, W. J. and S. L. H. Fuller. 1965. The genus *Viviparus* (Viviparidae) in North America. *Occasional Papers on Mollusks* **2**: 385-412.

Clench, W. J. and R. D. Turner. 1955. The North American Genus *Lioplax* in the Family Viviparidae. *Occasional Papers on Mollusks* **2**: 1-19.

Coleman, R. W. 1984. A preliminary survey on certain mollusks of Dickinson County, Iowa. *The Proceedings of the Iowa Academy of Science* **91**: 202.

Dazo, B. C. 1965. The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). *Malacologia* **3**: 1-80.

Dillon, R. T., Jr. 2000. *The Ecology of Freshwater Molluscs*. Cambridge University Press, Cambridge, United Kingdom.

Dillon, R. T. and A. R. Wethington. 2004. No-choice mating experiments among six nominal taxa of the subgenus *Physella* (Basommatophora: Physidae). *Heldia* **6**: 1-10.

Dillon, R. T., Jr., A. R. Wethington, J. M. Rhett, and T. P. Smith. 2002. Populations of the freshwater pulmonate *Physa acuta* are not reproductively isolated from American *Physa heterostropha* or *Physa integra*. *Invertebrate Biology* **121**: 226-234.

Dundee, D. S. 1957. Aspects of the biology of *Pomatiopsis lapidaria* (Say) (Mollusca: Gastropoda: Prosobranchia). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* **100**: 1-37.

Eckblad, J. W., N. L. Peterson, and K. Ostlie. 1977. The morphometry, benthos and sedimentation rates of a floodplain lake in pool 9 of the upper Mississippi River. *American Midland Naturalist* **97**: 433-443.

Euliss, N. H., Jr. and D. M. Mushet. 1999. Influence of agriculture on aquatic invertebrate communities of temporary wetlands in the prairie pothole region of North Dakota, USA. *Wetlands* **19**: 578-583.

Euliss, N. H., D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands of the prairie pothole region: Invertebrate species composition, ecology, and management. *In*: D. P. Batzer and S. A. Wissinger, eds., *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*. John Wiley and Sons, Inc., New York. Pp. 471-514.

Freshwater Mollusk Conservation Society. 2005. Committee on the Status and Distribution of Gastropods: The Freshwater Gastropods of North America. Available at: http://www. cofc. edu/~dillonr/fwgnahome. htm 8 February 2005.

Gale, W. F. 1975. Bottom fauna of a segment of pool 19, Mississippi River, near Fort Madison, Iowa 1967-1968. *Iowa State Journal of Research* **49**: 353-372.

Gale, D. D., E. E. Drevs, and M. P. Gross. 1972. The current status of the limnology and bottom fauna of Lakes West and East Okoboji. *The Proceedings of the Iowa Academy of Science* **79**: 17-24.

Haldeman, S. S. 1840-1845. *A Monograph of the Freshwater Univalve Mollusca of the United States: Including Notices of Species in Other Parts of North America*. E. G. Dorsey, Philadelphia.

Hershler, R. 1996. Review of North American aquatic snail genus

Probythinella (Rissoidea: Hydrobiidae). *Invertebrate Biology* **115**: 120-144.

Hershler, R. and F. G. Thompson. 1996. Redescription of *Paludina integra* Say, 1821, type species of genus *Cincinnatia* (Gastropoda: Hydrobiidae). *Journal of Molluscan Studies* **62**: 33-55.

Hershler, R., J. R. Holsinger, and L. Hubricht. 1990. A revision of the North American freshwater snail genus *Fontigens* (Prosobranchia: Hydrobiidae). *Smithsonian Contributions to Zoology* **509**: 1-49.

Hubert, W. H., G. E. Darnell, and D. E. Dolk. 1984. Late-winter abundance and substrate associations of benthos in pool 13, upper Mississippi River. *The Proceedings of the Iowa Academy of Science* **91**: 147-152.

Jokinen, E. H. 1982. *Cipangopaludina chinensis* (Gastropoda: Viviparidae) in North America, review and update. *The Nautilus* **96**: 89-95.

Jokinen, E. H. 1983. *The Freshwater Snails of Connecticut*. State Geological and Natural History Survey of Connecticut, Department of Environmental Protection Bulletin 109, Hartford, Connecticut.

Jokinen, E. H. 1992. *The Freshwater Snails (Mollusca: Gastropoda) of New York State*. New York State Museum Bulletin 482, Albany, New York.

Jude, D. J. 1973. Food and feeding habits of gizzard shad in pool 19, Mississippi River. *Transactions of the American Fisheries Society* **102**: 378-383.

Kater, S. B. and C. R. S. Koneko. 1972. An endogenously bursting neuron in the gastropod mollusc, *Helisoma trivolvis*: Characterization of activity *in vivo*. *Journal of Comparative Physiology* **79**: 1-14.

Kennedy, J. O. and J. G. Miller, III. 1990. A survey of the benthic macroinvertebrates of the Big Spring Basin, Iowa. *The Journal of the Iowa Academy of Science* **97**: 46-54.

Kessel, R. G. and H. W. Beams. 1984. Intracisternal tubules and intramitochondrial filaments in cells of a snail, *Lymnaea stagnalis*. *Tissue and Cell* **16**: 405-410.

Keyes, C. R. 1888. An annotated catalogue of the Mollusca of Iowa. *Bulletin of the Essex Institute* **20**: 61-83.

Martin, S. M. 1999. Freshwater snails (Mollusca: Gastropoda) of Maine. *Northeastern Naturalist* **6**: 39-88.

Meierhoff, M. L. and S. D. Prill. 1982. A survey of the benthic macroinvertebrates of the upper Iowa River basin. *The Proceedings of the Iowa Academy of Science* **89**: 89-98.

Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of the aquatic mollusks in the southeastern United States: A downward spiral of diversity. *In*: G. W. Benz and D. E. Collins, eds., *Aquatic Fauna in Peril*, Southeast Aquatic Research Institute Special Publication 1, Lenz Design and Communications, Decatur, Georgia. Pp. 43-85.

Pilsbry, H. A. 1886. Notes on some eastern Iowa snails. *American Naturalist* **20**: 72-77.

Pilsbry, H. A. 1898. Notes on new and little-known Amnicolidae. *The Nautilus* **12**: 42-44.

Pratt, W. H. 1876. List of land and fresh water shells found at Davenport, Iowa. *Proceedings of the Davenport Academy of Natural Sciences* **1876**: 165-168.

Prior, J. C. 1991. *Landforms of Iowa*. University of Iowa Press, Iowa City, Iowa.

Prior, J. C., J. L. Boekhoff, M. R. Howes, R. D. Libra, and P. E. VanDorpe. 2003. *Iowa's Groundwater Basics*. Iowa Department of Natural Resources, Iowa City, Iowa.

Rausch, C. G. and R. V. Bovbjerg. 1973. Fauna of the middle Little Sioux River and comparison with upper and lower regions. *The Proceedings of the Iowa Academy of Science* **80**: 111-116.

Say, T. 1817. Descriptions of new species of land and fresh water shells. *Journal of the Academy of Natural Sciences of Philadelphia* **1**: 123-126.

Say, T. 1821. Descriptions of univalve shells of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* **2**: 149-179.

Say, T. 1832. *American Conchology, or Descriptions of the Shells of North America, Illustrated by Colored Figures. Part IV*. New Harmony, Indiana.

Shimek, B. 1890. The Mollusca of eastern Iowa. *Bulletin of the State University of Iowa* **1**: 56-81.

Shimek, B. 1893. Additional notes on Iowa Mollusca. *The Proceedings of the Iowa Academy of Science* **1**: 107-111.

Shimek, B. 1915. The Mollusca of the Okoboji region. *Bulletins from the Laboratories of Natural History* **7**: 70-88.

Shimek, B. 1935a. The effect of pollution on mollusks in Iowa. *The Nautilus* **48**: 109-111.

Shimek, B. 1935b. *Ferrissia* in the lake region of Iowa. *The Nautilus* **49**: 44-46.

Simpson, C. T. 1895. *Pleurocera subulare* in water-mains. *The Nautilus* **9**: 37-38.

Smith, D. G. 2000. Notes on the taxonomy of introduced *Bellamya* (Gastropoda: Viviparidae) species in northeastern North America. *The Nautilus* **114**: 31-37.

Stewart, T. W. and R. T. Dillon, Jr. 2004. Species composition and geographic distribution of Virginia's freshwater gastropod fauna: A review using historical records. *American Malacological Bulletin* **19**: 79-91.

Stimpson, W. 1865. *Researches Upon the Hydrobiinae and Allied Forms*. Smithsonian Miscellaneous Collections 201, Washington, DC.

Te, G. 1975. Michigan Physidae, with systematic notes on *Physella* and *Physodon*. *Malacological Review* **8**: 7-30.

Thompson, D. 1973. Feeding ecology of diving ducks on Keokuk Pool, Mississippi River. *Journal of Wildlife Management* **37**: 367-381.

Thompson, F. G. 1977. The hydrobiid snail genus *Marstonia*. *Bulletin of the Florida State Museum, Biological Sciences* **21**: 113-158.

Thompson, F. G. 1984. North American freshwater snail genera of the hydrobiid subfamily Lithoglyphinae. *Malacologia* **25**: 109-141.

Tobin, G. A. 2000. Geographical overview and configuration: An analysis of the natural landscape. *In*: F. H. Gille, N. Capace, and T. F. Gille, eds., *The Encyclopedia of Iowa*, Vol. 1. Somerset Publishers, Inc., St. Clair Shores, Michigan. Pp. 11-22.

Tryon, G. W. 1863. Notes on American fresh water shells. *Proceed-*

ings of the Academy of Natural Sciences of Philadelphia **1863**: 451-452.

Tryon, G. W. 1865. Catalogue of the Mollusca, collected by Prof. D. S. Sheldon, at Davenport, Iowa. *American Journal of Conchology* **1**: 68-70.

Tryon, G. W. 1870-1871. *A Monograph of the Fresh-water Univalve Mollusca of the United States.* Conchological Section of the Academy of Natural Sciences, Philadelphia, Pennsylvania.

Turgeon, D. D., J. F. Quinn, Jr., A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione, and J. D. Williams. 1998. *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks.* American Fisheries Society Special Publication 26, Bethesda, Maryland.

Ulmer, M. J. 1960. *Physa sayii*, a new intermediate host for the turtle lung fluke, *Heronimus chelydrae* (Trematoda: Heronimidae). *Journal of Parasitology* **46**: 813-814.

Ulmer, M. J. and S. C. Sommer. 1957. Development of sporocysts of the turtle lung fluke, *Heronimus chelydrae* MacCallum (Trematoda: Heronimidae). *The Proceedings of the Iowa Academy of Science* **64**: 601-613.

U. S. Fish and Wildlife Service. 2005. U.S. Listed Invertebrate Animal Species by Taxonomic Group. Available at: http://ecos . fws. gov/tess_public/TESSWebpage 8 February 2005.

Van Cleave, H. J. and R. Chambers. 1935. Studies on the life history of a snail of the genus *Lioplax*. *American Midland Naturalist* **16**: 913-920.

van der Schalie, H. and D. S. Dundee. 1955. The distribution, ecology, and life history of *Pomatiopsis cincinnatiensis* (Lea), an amphibious, operculate snail. *Transactions of the American Microscopical Society* **74**: 119-133.

Walker, B. 1902. A revision of the carinate valvatas of the United States. *The Nautilus* **15**: 121-125.

Walker, B. 1904. Notes on American Ancyli. III. *The Nautilus* **18**: 75-83.

Walker, B. 1909. Notes on *Planorbis* II: *P. bicarinatus*. *The Nautilus* **23**: 21-32.

Walker, B. 1918. A synopsis of the classification of the freshwater Mollusca of North America, North of Mexico, and a catalogue of the more recently described species, with notes. *University of Michigan Museum of Zoology Miscellaneous Publications* **6**: 1-213.

Witter, F. M. 1878. List of Mollusca collected at Muscatine, Iowa. *Journal of Conchology* **1**: 383-394.

Wurtz, C. B. 1949. *Physa heterostropha* (Say). *The Nautilus* **63**: 20-33.

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